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RESPONSE OF GERMAN COCKROACHES TO A DISPERSANT AND OTHER SUBSTANCES SECRETED BY CROWDED ADULTS AND NYMPHS (BLATTODEA: BLATTELLIDAE)

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Abstract.—The responses of adult male German cockroaches to filter papers conditioned by crowded adult males and by large nymphs is compared to their response to female-conditioned papers. Males were repelled only from the latter papers. The lack of repellency to papers conditioned by males and large nymphs may be attributed to insufficient amounts of a dispersant pheromone to counteract the response to aggregation pheromone.

Chemical cues mediate defensive, reproductive, and social behaviors in insects. For example, aggregations are pheromonally induced in the crickets *Ceuthophilus secretus* (Nagel and Cade, 1983), *Acheta domestica* (Sexton and Hess, 1968; McFarlane et al., 1983), locusts (Gillett, 1968) and the cockroach, *Blattella germanica* (L.) (Bell et al., 1972; Ishii, 1970; Ishii and Kuwahara, 1967; Rust and Appel, 1985). In *A. domestica* (Sexton et al., 1968) and *B. germanica* (Suto and Kumada, 1981), the response to aggregation pheromone is countered by repellent effects of a dispersant which, in *A. domestica,* is secreted by both adult males and females. In *B. germanica* the dispersant was detected in bioassays where filter paper was conditioned by crowding adults of both sexes. Further study indicated the dispersant is present in oral secretions and is probably a proteinaceous substance(s) (Nakayama et al., 1984).

Nymphs of all stages, adult males, and gravid and non-gravid females were repelled from papers conditioned by crowded adult females, indicating all members of a population would respond to the dispersant (Ross and Tignor, 1985). The purpose of the present experiment was to determine whether cockroaches would also be repelled from papers conditioned by crowded adult males or large nymphs and to compare the response to that from female-conditioned papers. Adult males were used to test for repellency because they showed a particularly strong response to female-conditioned papers (Ross and Tignor, 1985).

Materials and Methods

Cockroaches were drawn from the VPI wild-type strain. It has been maintained in our laboratory for approximately 160 generations. The laboratory is on a 14D/10L photocycle with temperature range of 24–27°C. Our bioassay technique was patterned after that of Ishii et al. (1967) and Suto and Kumada (1981). It differed from the experimental design we used to test response of different age/sex classes to female-conditioned paper (Ross and Tignor, 1985) in that data were recorded by visual observation rather than photography and bioassays were conducted in the laboratory rather than a dark chamber. Therefore, to make results from crowded adult males and large nymphs as comparable as possible to those from females, an additional experiment was conducted with crowded adult females.

Three filter papers were used in the bioassays. One was conditioned by 40 adult males, one by 50 large nymphs (6th instar), and the third was unconditioned (control). Conditioning was done during the first 2–3 h of the light period by holding either the adult males or large nymphs for 1 h in a plastic vial (2.9 diam. × 5.5 cm in height) that contained a strip of Whatman no. 1 filter paper (3.8 × 7.0 cm) folded into a W-shape. The conditioned and control papers were placed on end equal distances between edges on the bottom of a glass battery jar (14.5 diam. × 19.5 cm in height). Papers were attached to the jar using a small drop of Liquid Paper®. Their positions were randomized. The jar top was covered with cheese cloth and the exterior of the jar with paper towels. Tests were begun immediately after conditioning. Twelve 2–3 week-old adult males were released into the jar. Their distribution was recorded visually at 30 min intervals during a period of 4 h. The experiment was replicated 18 times. Comparable data on response to papers conditioned by adult females were obtained by conditioning one paper with 30 gravid and the other with 30 7–10 day-old non-gravid females (probably mated). Otherwise the procedures were the same as above. Conditioning by larger numbers of males and nymphs than females assured a near equal degree of spatial crowding since their body size is somewhat smaller than that of females.

The data were subjected to aricsine and analyzed using Tukey's studentized range test (Sokal and Rohlf, 1969). Analysis was on the mean percent of males on the three papers through the period from 90 to 240 min because it took approximately 90 min for the adult males to settle on the filter papers.

Results and Discussion

Figs. 1 and 2 show that most of the males were on filter papers, as expected since German cockroaches prefer vertical to flat surfaces (Bell et al., 1972; Rust and Appel, 1985). They were neither strongly attracted to nor strongly repelled from papers conditioned by large nymphs and other adult males (Fig. 1). In contrast, the majority of the males were on the control paper in the experiment with papers conditioned by gravid and non-gravid females (Fig. 2), indicating they were repelled from the conditioned papers (mean 94.9% on the control period through the period from 90–240 min; $P < 0.05$). Although Fig. 1 shows a more equal distribution of males, the mean proportion on paper conditioned by large nymphs (36.4 ± 2.8% SE) was significantly higher than that on either the male-conditioned (23.3 ± 2.2% SE) or control (20.8 ± 2.8% SE) papers ($90 < \text{time} < 240$ min). The proportions on the male-conditioned and control papers did not differ significantly. The similarity between these estimates reflects a tendency for a larger cluster of males to occur on the control paper with equal frequency to the conditioned paper, rather than a 50:50 division between the distribution of individuals with each replicate. For example, in 13 of 18 replicates, >75% of the males in these locations were on one or the other paper.

The lack of repellency of paper conditioned by large nymphs and adult males seems contradictory to experiments of Nakayama et al. (1984) that indicated adult

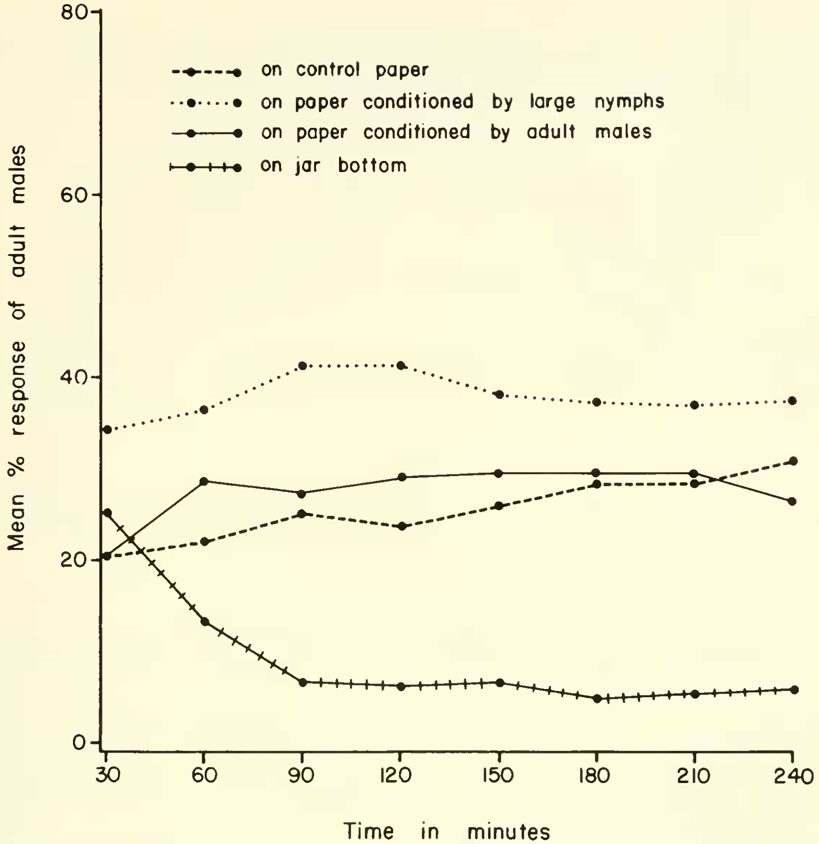

Fig. 1. Distribution of adult male *B. germanica* in battery jars containing filter papers conditioned by crowding adult males and large nymphs and an unconditioned (control) paper.

males and large nymphs secrete the dispersant. However, their procedures differed from those used here in the following respects: the response of small nymphs, rather than adult males, was tested; larger numbers were used to obtain the dispersant; and the papers were not conditioned directly by the insects. The former two differences probably did not contribute to the apparent discrepancy. German cockroaches respond to the dispersant regardless of age/sex class (Ross and Tignor, 1985). The effects of increased crowding have not been completely explored, but no indication of repellency was found in preliminary tests with extreme crowding of adult males (Ross and Tignor, unpubl.). For example, of 90 small nymphs tested against a control and a paper conditioned by 75 males, 59% were on the conditioned paper. On the other hand, the differing results can be explained readily by conditioning procedures. Nakayama et al. (1984) rinsed jars contaminated by crowded insects with Tris-HCl buffer, followed by extraction in ethyl ether. The remaining "aqueous solution" was used to condition papers. Aggregation pheromone is removed in ethyl ether (Ishii and Kuwahara, 1967). We infer that the results of our experiments reflect response to a combination of dispersant and aggregation pheromone, whereas those of Nakayama et al. (1984) tested for dispersant emission.

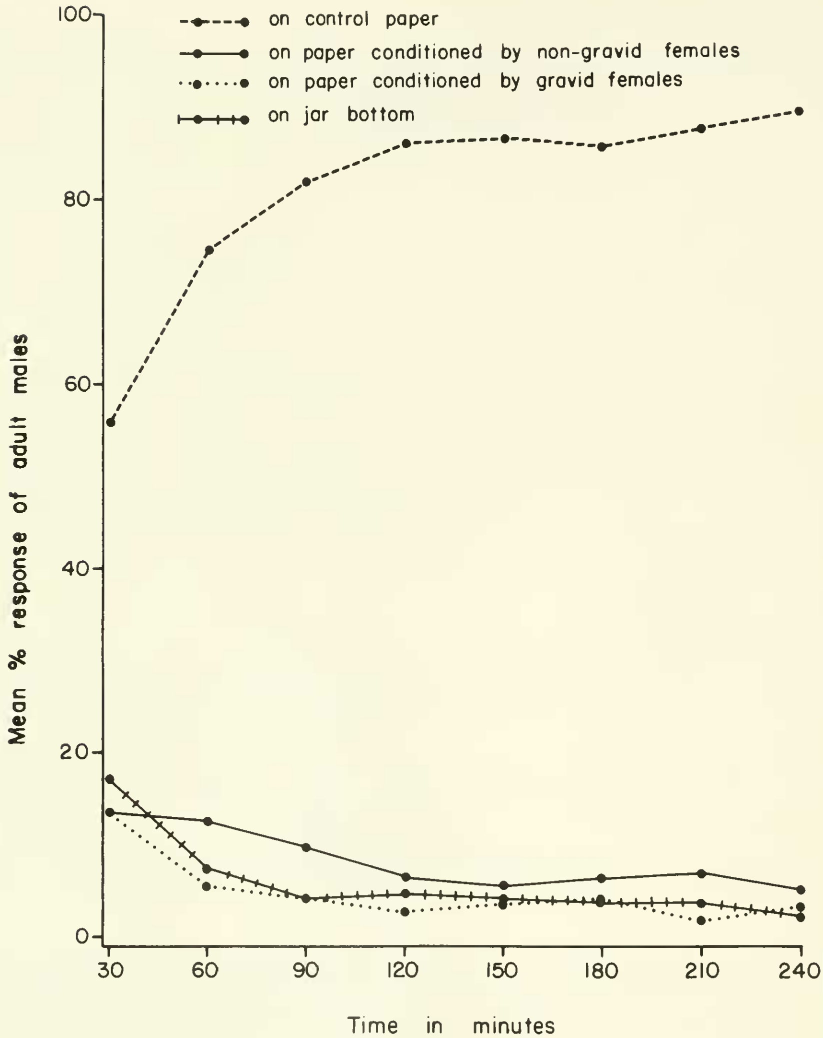

Fig. 2. Distribution of adult male *B. germanica* in battery jars containing filter papers conditioned by crowding gravid and non-gravid females and an unconditioned (control) paper.

The results reported here leave little doubt that the repellency of papers conditioned by adults in Suto and Kumada's (1981) bioassays was due solely to the secretion of the dispersant pheromone by adult females. Conditioned filter papers showed the characteristic wetness that Suto and Kumada associated with secretion of the dispersant. However, this secretion was repellent only in the case of female-conditioned papers. Unfortunately, Suto and Kumada's evidence that adults secrete aggregation pheromone "irrespective of population density" does not shed light on the relative roles of aggregation pheromone and the dispersant in the observed differences between the response to female- and male-conditioned papers. The possibility that adult females secreted such large amounts of the dispersant that response to aggregation pheromone was over-ridden cannot be distinguished from the alternate possibility that they ceased or decreased secretion of aggregation pheromone when crowded. Likewise, the absence of a detectable response of adult males to male-conditioned paper could have several explanations. They secrete aggregation pheromone under presumably uncrowded conditions (Ishii and Kuwahara, 1967) and are capable of producing the dispersant (Nakayama et al., 1984). Possibly neither substance was present on conditioned paper in an amount sufficient to obscure response to the other substance. Alternatively, it may be that adult males cease secretion of both pheromones when crowded. The attraction of males to paper conditioned by large nymphs was almost certainly a response to aggregation pheromone. The confinement of the insects in a small vial ensured a fairly intense level of crowding, yet only the adult females secreted sufficient dispersant to elicit a repellent effect. We suggest that adult females give the signal that causes aggregations to disperse from crowded and perhaps other stressful conditions.

Acknowledgments

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